Imaging the interaction of roots and phosphate fertiliser granules using 4D X-ray tomography

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Use of a coupled soil-root-leaf model to optimise phosphate fertiliser use efficiency in barley

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Abstract: (~~200~~192/200)

Aims Phosphorus (P) is an essential nutrient necessary for maintaining crop growth, however, it's often used inefficiently within agroecosystems, driving industry to find new ways to deliver P to crops sustainably. We ~~consider a precision agriculture approach which~~aim to combine~~s~~ traditional soil and crop measurements with climate-driven mathematical models, ~~that can~~to optimise the timing and placement of fertiliser applications.

Methods The whole plant crop model combines an above-ground leaf model with an existing spatially explicit below-ground root-soil model to estimate plant P uptake and leaf mass. We let P-dependent photosynthesis estimate carbon (C) mass, which in conjunction with temperature sets the root-growth-rate.

Results The addition of the leaf model achieved a better estimate of two sets of barley field trial data for ~~leaf mass and~~ plant P uptake, compared with just the root-soil model alone. Furthermore,

discrete fertiliser placement increases plant P uptake by up to 10% in comparison to incorporating fertiliser.

Conclusions By capturing essential plant processes we are able to accurately simulate P and C use and water and P movement during a cropping season. The powerful combination of mechanistic modelling and experimental data allows physiological processes to be quantified accurately and useful agricultural predictions for site specific locations.

Keywords Mathematical modelling, phosphate, phosphorus, fertiliser strategy, barley field study, above and below ground

Introduction

The world-wide production of food has increased due to the demands of an ever expanding global human population (Brown, 2012). Due to the lack of land available for agricultural expansion, there is a need to increase yields sustainably by manipulating the existing environment in which crops are grown, and breeding more resource efficient crops. Resource management for arable farming systems is critical to the survival of the human population and large amounts of money and time are needed to elicit the appropriate improvements (Conway and Barbier, 1990).

Phosphorus (P) is one of the essential nutrients required for plant growth and plays an important role in photosynthesis, respiration, and seed and fruit production.

We are interested in how crops grow and survive in low P environments and how fertiliser and soil cultivation methods are influencing crop performance. A number of studies have considered the response of adding different amounts and rates of fertiliser P; in some soils large effects are seen whereas no effect is seen in others (Bolland and Baker, 1998; Kuchenbuch and Buczko, 2011; Valkama et al., 2011). There are many ways one could apply P to soils; for example incorporating (also known as broadcasting, involves an even spreading of P on top of the soil), placing (also known as banding, involves injecting P into the soil nearer the rooting zone either in row or between rows)

or as a coating on seeds. Studies have shown that injecting fertiliser into the soil nearer to the root zone (placing) increases plant P uptake compared to incorporated P (Randall and Hoeft, 1988; Lohry, 1998; Owusu-Gyimah *et al.,* 2013). In addition, studies have been conducted to estimate the differences in soil cultivation methods on plant P uptake; for example, conventional plough *versus* minimum tillage (also considering gene variation, George *et al.,* 2011). The idea behind ploughing is to turn over or mix the top 25 cm of soil to loosen the soil for seeding, bury any existing crop residues or weeds, and to provide a good distribution of nutrients for the coming crop. This is in contrast to minimum tillage which enhances topsoil stability against erosion, retains moisture and reduces crop establishment costs, but segregates P content with depth and can leave 30% of crop residue on the soil surface.

Due to the rising cost of fertilisers and agricultural machinery, crop production has become a multi-objective optimisation problem to minimise multiple costs while trying to maximise the crop yield and environmental impact of fertilisers. This is a complex problem due to varying climatic conditions, an abundance of technological machines, and availability of more data concerning the states of fields than ever before. Precision agriculture is an emerging field involved with combining the newest technologies to the farming industry, ranging from unmanned drone maps of fields to computer-assisted tractors (Blackmore, 2014). This new technology is enabling automated real time decision making, applying the most effective treatment to crops at the best time for the best price. Mathematical models, supported by experimental data, are needed to help predict best decisions in the short term, and also strategically, to optimise between possible future options. Whilst such models are ~~seldom~~ not always commercially used~~employed at present~~, their potential capabilities are attractive, given that field-scale experiments are both costly and time-consuming, and integration and dissemination of their empirical results is challenging (Selmants and Hart, 2010; Jeuffroy *et al.,* 2012; Sylvester-Bradley, 1991).

A plethora of models exist that describe the processes involved in plant growth and the behaviour of nutrients and water in the soil. Each model has its own unique assumptions and is generally targeted at specific scientific problems within the area of agriculture. For example, Greenwood *et al.* (2001) developed a dynamic model (PHOSMOD) for the effects of soil P and fertiliser P on crop growth, P uptake and soil P in arable cropping; ~~-~~ Jones *et al.* (2003) describe a decision support system for agrotechnology transfer (DSSAT) which focuses on average plant-environment interactions; and Keating *et al*. (2003) review an agricultural production systems simulation (APSIM) developed in CISRO, Australia which deals with water, N, P, pH, erosion and management issues. At the beginning of the 21st century, modelling 3D architectures of plant roots (RootBox, ROOTMAP, SimRoot, RootTyp, SPACSYS, R-SWMS) has become popular (Dunbabin *et al.,* 2013). In addition, two research groups that model above ground 3D plant structures, Prunsinkiewicz Algorithmic Botany group at the University of Calgary and the Andrieu group (ADEL-wheat model), both use L systems to simulate the above ground structure of wheat plants. L systems, introduced by Lindenmayer in 1968, represent a string of production rules that are used to create geometric structures, ideal for plant development. However all these models do not describe the root-soil interaction explicitly and do not fully integrate functions that occur above ground with ones that occur below ground. Therefore plants of the same genotype are represented alike and phenotypic differences cannot be observed. We hope to address some of these problems by creating a model that links the above and below ground processes in such a way that they rely on one another. Our whole crop model is based on a below ground plant-soil interaction model (Roose and Fowler, 2004b; Heppell *et al.,* 2015) coupled with an above ground leaf growth model based on the seminal work of Thornley (1995).

Here we describe a whole crop model that includes a below-ground root model and an above-ground leaf model and which is validated against experimental data on barley with a varying P fertiliser scenario analysis. The development of the model is seen as a step-change in our computational capability to help predict soil P supply, crop P uptake patterns and fertilizer requirements.

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Materials and Methods

Experimental data

Two barley field trial data sets are used, consisting of leaf mass and plant P uptake values at different growth stages (GS31, GS45 and GS91 for spring barley; GS39 and GS92 for winter barley). The experimental data includes different rates of P application (0, 5, 10, 20, 30, 60, 90 kg P ha^{-1} for spring barley; 0 15, 30, 60, 90, 120 kg P ha^{-1} for winter barley) and both sites were classified with an Olsen P index 1 soil. The protocol for this is described in Heppell *et al.* (2015). In addition, we use the climate data, from the UK Met office Integrated Data Archive System (MIDAS), to accompany the spring barley (Inverurie, Scotland) and winter barley (Cambridge, England) data sets for the specific fields in the trial. The climate data consists of daily values for mean temperature (°C), rainfall (mm), wind speed (m s^{-1}) and humidity (%).

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Modelling the whole crop

In this paper we extend a root-soil model (Roose and Fowler, 2004b; Heppell *et al.,* 2015) which estimates plant P uptake, with an above ground model which estimates leaf mass (based on Thornley, 1995), to produce a whole crop model. We first describe the root-soil model (hereafter called the root model), followed by the leaf model and then our coupling process to create a whole crop model.

Root and soil model

To model the root system we follow the same approach as described in Roose *et al.* (2004b) and Heppell *et al.* (2015) by modelling two orders of root branches only (main and first order branches). First order roots branch off the main order roots at a given density (ψ_1), branching angle (θ), and each order of roots has a given maximum length and radius (L_0, L_1 and a, a_1 for main and first order roots, respectively). As in Roose *et al.* (2004b) and Heppell *et al.* (2015) we let the root growth slow

down as the root becomes longer. Following Heppell *et al.* (2015) we also let the root growth rate (r) be dependent upon temperature *T*,

Eqn. 1 $$\frac{\partial l_i}{\partial t} = r(T(t))\left(1 - \frac{l_i}{L_i}\right),$$

where l_i is the current length of an order i root and L_i is the maximum length of an order i root.

The root-soil model is described by the following two equations for water saturation (Eqn. 2) and P (Eqn. 3) concentration respectively,

Eqn. 2 $$\phi \frac{\partial S}{\partial t} = \nabla \cdot \left[D_0 D(S) \nabla S - K_S k(S) \widehat{\boldsymbol{k}}\right] - F_w(S, z, t)\ ,$$

Eqn. 3 $$\frac{\partial}{\partial t}[(b + \phi S)c] + \nabla \cdot [c\boldsymbol{u}] = \nabla \cdot \left[D_f \phi^d S^d \nabla c\right] - F(c, z, t)\ ,$$

where the water flux in the soil, $\boldsymbol{u}$, is given by Darcy's law,

Eqn. 4 $$\boldsymbol{u} = -D_0 D(S) \nabla S + K_S k(S) \widehat{\boldsymbol{k}}.$$

In the above equations S is the relative water saturation given by $S = \phi_1/\phi$, ϕ_1 is the volumetric water content, and ϕ is the porosity of the soil. D_0 (cm^2 day^{-1}) and K_S (cm day^{-1}) are the parameters for water 'diffusivity' and hydraulic conductivity, respectively (Van Genuchten, 1980). $D(S)$ and $K(S)$ characterize reduction in water 'diffusivity' and hydraulic conductivity in response to the relative water saturation decrease, where the functional forms for partially saturated soil are given by Van Genuchten (1980). $\widehat{\boldsymbol{k}}$ is the vector pointing vertically downwards from the soil surface and F_W is the water uptake by the plant root system per unit volume of soil as given by Roose and Fowler (2004a).

For the total P conservation (Eqn. 3), c is the P concentration in soil pore water, b is the soil buffer power characterising the amount of P bound to the soil particle surfaces, D_f is the P diffusivity in free water and d is an impedance factor; $1 \leq d \leq 3$ (Barber, 1984; Nye and Tinker, 1977). $F(c, S, t)$ describes the rate of plant P uptake by a root branching structure (Roose *et al.,* 2001). Both F_w and F

are affected by the spatially and temporally evolving root structure. Water is only taken up by the main order roots while P is taken up by all roots; see Roose and Fowler (2004b) for details of the derivation. The equation for F_w is given by,

Eqn. 5 $$F_W = \frac{2\pi a_1 k_r + (2\pi a_1 k_r k_z)^{\frac{1}{2}} \psi_1(z)}{\pi(a + L_1 cos\theta)^2}[-p_c f(S) - p_r],$$

where ψ_1 is the density of first order roots on the main order roots, a_1 is the first order root radius, a is the main order root radius, L_1 is the maximum length of the first order branches, θ is the angle between the main root and the first order branches, k_r is the root radial water conductivity parameter (m s^{-1} Pa^{-1}), k_z is the root axial hydraulic conductivity calculated using Poiseuille law (m^4 Pa^{-1} s^{-1}), p_c (Pa) is a characteristic suction pressure determined from experimental data for different types of soil, $f(S) = \left(s^{-1/m} - 1\right)^{1-m}$, where m is the Van Genuchten soil suction parameter (where $0 < m < 1$), and p_r is the root internal xylem pressure (Pa).

Root internal xylem pressure (p_r) is calculated by balancing radial and axial fluid fluxes inside the root, i.e. after Roose and Fowler (2004a) we have,

Eqn. 6 $$2\pi a k_r(-p_c f(S) - p_r) = -k_z \frac{\partial^2 p_r}{\partial x^2},$$

with two boundary conditions; an impermeable root tip (Eqn. 7) and a root internal pressure (P) at the base of the zero order root (Eqn. 8),

Eqn. 7 $$\frac{\partial p_r}{\partial x} = 0 \text{ at } x = L,$$

Eqn. 8 $$p_r = P \text{ at } x = 0,$$

where P is a function of temperature (T), humidity (H) and a base line pressure (p_r^0) for fitting parameters λ_1, λ_2 and λ_3 (see Heppell *et al.,* 2014 for the procedure to estimate them), i.e.

Eqn. 9 $$P = (p_r^0 + \lambda_3) + \lambda_1 T + \lambda_2 H.$$

163 The rate of plant P uptake is given by,

164 Eqn. 10 $$F(c,z,t) = \frac{F_0+F_1}{\pi(a+L_1 cos\theta)^2},$$

165 where F_0 and F_1 are the uptake rates for zero and first order roots derived in Roose *et al.* (2004b).

166 The boundary conditions to accompany Equations 1 and 2 include a soil surface boundary condition
167 for water,

168 Eqn. 11 $$-D_o D(S)\frac{\partial S}{\partial z} + K_S k(S) = W_{dim} \text{ at } z = 0.$$

169 W_{dim} (the flux of water into the soil) is dependent upon rainfall (R), humidity (H), temperature (T),
170 wind speed (WS) and a constant (E) which sets a base line flux i.e.

171 Eqn. 12 $$W_{dim} = \delta R + \alpha H + \beta T + \gamma WS + E,$$

172 for fitting parameters δ, α, β and γ (see Heppell *et al.,* 2014 for how these values were estimated).

173 In addition, we have a boundary condition for the concentration of P (c) at the soil surface,

174 Eqn. 13 $$-D_f \phi^d S^d \frac{\partial c}{\partial z} + W_{dim} c = 0 \text{ at } z = 0, \text{ for } t > 0.$$

175 We set a zero flux at the bottom of the soil (l_W) for both P and water,

176 Eqn. 14 $$-D_o D(S)\frac{\partial S}{\partial z} + K_S k(S) = 0 \text{ at } z = l_W,$$

177 Eqn. 15 $$-D_f \phi^d S^d \frac{\partial c}{\partial z} = 0 \text{ at } z = l_W.$$

178 The initial state of P concentration and water saturation in the soil is given where possible by the
179 initial soil data for the spring and winter barley experimental sites. A uniform water saturation
180 profile is initially set at $S = 0.3$ for the two experimental sites; however for the initial P
181 concentration ($c_0(z)$) we consider two different cases; (1) a uniform concentration and (2) an
182 exponentially decaying concentration:

183 Eqn. 16

$$\begin{array}{lll} (1) & c_0(z) = & c_A \quad \text{at } t = 0, \forall z \\ (2) & c_0(z) = & A_1 e^{-B_1 z} \quad \text{at } t = 0, \forall z' \end{array}$$

184 where c_A is set to 16 mg P l^{-1}, $A_1$is the P concentration at the top of the soil (23 mg P L^{-1}) and B_1 is
185 the strength of the decay in the concentration of P (0.345). The initial P concentration values (C_A,
186 $A_1$and B_1) come from a best fit to the data sets in Heppell et al., (2015) and are both classified as an
187 Olsen P index 1 soil (Defra, 2010). To reflect the different fertiliser scenarios being used at each field
188 site a set amount of P (P_1) (0-120 kg P ha^{-1}) was either applied at the surface ($z = 0$) (P broadcast) or
189 at a set depth below the soil (D_1) (P placement).

190 Eqn. 17

$$\begin{array}{c} c = c_0(z) + H(z), \\ \begin{array}{lll} (\text{broadcast}) & H(z) = P_1 & \text{at } t = 0, \quad z = 0 \\ (\text{placement}) & H(z) = P_1 & \text{at } t = 0, \quad z = D_1 \\ (\text{else}) & H(z) = 0 & \text{at } t = 0 \quad \forall z \end{array} \end{array}.$$

191 **Leaf growth model**

192 We have altered a compartmental model developed by Thornley (1995) to describe leaf mass M_L
193 (kgL), leaf C M_C (kgC) and leaf P M_P (kgP) as well as the concentration of free C $[C] = M_C/M_L$ (kgC
194 kgL^{-1}) and free P $[P] = M_P/M_L$ (kgP kgL^{-1}) dynamics within the leaves. The leaf model takes into
195 account non-linear dynamics of formation of leaf litter and leaf self-shading. Additionally we have
196 made photosynthesis dependent upon P content in the plant (Foyer and Spencer, 1986, Wissuwa *et*
197 *al.*, 2005) and we have altered the leaf growth term, G_{sh}, which was dependent on [C] and [P], to
198 also depend upon ~~the~~ air temperature (A_T)~~,~~ for ~~the~~ winter barley but not spring barley~~), as well as [C]~~
199 ~~and [P]~~. We don't let air temperature affect spring barley as the growing season is much shorter
200 compared to winter barley and it is not needed for a good fit to the experimental data. The
201 governing equations are given below and are represented in a flow diagram on Figure 1, i.e., we
202 have

203 Eqn. 18

$$\frac{\partial M_L}{\partial t} = \overbrace{\widetilde{G_{sh}}}^{\text{Leaf growth rate}} - \overbrace{\frac{K_{litt}}{1+\frac{K_{mlitt}}{M_L}} M_L}^{\text{Leaf metabolism/litter}},$$

Eqn. 19 $$\frac{\partial M_C}{\partial t} = \overbrace{\varepsilon k_1[P]}^{\text{Production of C from photosynthesis}} - \overbrace{f_c G_{sh}}^{\text{Use of C for L growth}} - \overbrace{\beta_c[C]}^{\text{Output of C to phloem}},$$

Eqn. 20 $$\frac{\partial M_P}{\partial t} = \overbrace{-f_p G_{sh}}^{\text{Use of P for L growth}} + \overbrace{F(c,z,t)}^{\text{Input of P from xylem}} - \overbrace{\beta_p[P]}^{Output\ of\ P\ to\ phloem} - \overbrace{k_p \varepsilon[P]k_1}^{Use\ of\ P\ to\ produce\ C},$$

where,

Eqn. 21 $$G_{sh} = k_G M_L[C][P]\frac{A_T^{s_1}}{s_2^{s_1} + A_T^{s_1}},$$

Eqn. 22 $$\varepsilon = \frac{k_C M_L}{\left(1+\frac{M_L}{k_M}\right)\left(1+\frac{[C]}{J_C}\right)},$$

where k_g is the leaf growth rate, K_{litt} is the litter rate, K_{mlitt} is the litter Michaelis-Menten constant, K_C is the photosynthesis rate, k_M is the constant accounting for the leaf self-shading, J_C is the C product inhibition constant, f_c is the fraction of total C used for leaf growth, f_p is the fraction of total P used for leaf growth, k_1 is the amount of P used for photosynthesis, $k_p k_1$ is the P loss due to photosynthesis, β_c is the rate of C output from the xylem to the phloem, β_p is the rate of P output to the phloem, $F(c,z,t)$ is the rate of P entry from the xylem (Eqn. 10) and s_1 and s_2 are fitting parameters. Initial values for the leaf (M_L), C (M_C) and P (M_P) mass are 1×10^{-4}, 0 and 1×10^{-7} kg respectively.

Whole crop model

In order to provide feedback between the root model and leaf model, we allow C mass to affect the root growth rate. Increasing C mass will increase root growth which in turn will increase plant P uptake. Through the process of photosynthesis, increasing plant P uptake will also increase C mass, thus creating a positive feedback loop.

The order i root growth rate is now dependent on C as well as temperature, therefore we replace Eqn. 1 with,

Eqn. 23 $$\frac{\partial l_i}{\partial t} = r(T,C)\left(1 - \frac{l_i}{L_i}\right),$$

where the rate of growth $r(T,C)$ is given by a function of temperature multiplied by a function of C ($r(T,C) = f(C)g(T)$),

Eqn. 24 $$f(C) = \frac{\alpha_C M_C}{\gamma_C + M_C},$$

Eqn. 25 $$g(T) = \begin{cases} 0 & T \leq 5^oC \\ A(T-5) & T > 5^oC \end{cases},$$

where γ_C is the mass of C when the root system is at half its maximum size, α_c is the strength of the C effect and A is a fitting parameter determining the strength of temperature dependence on root growth rate. Below critical temperature (5°C) there is no root growth and this reflects cold periods over the winter (Sylvester-Bradley *et al*., 2008).

~~Fitting process~~Calibration

The parameter list for the models above is given in Table 1. A subset of these parameters are fitted to the experimental data and their values can be seen in Table 2. To begin the ~~fitting procedure~~calibration process, the leaf model is first fit against the experimental leaf mass data, by 6 parameters (β_c, k_1, f_c, f_p for spring barley and in addition s_1 and s_2 for winter barley). In the leaf model only, we set the rate of P entry from the xylem ($F(c,z,t)$, Eqn. 10) proportional to the experimental plant P uptake to simulate a representative plant P root uptake. We then combine the models, i.e. let the rate of P entry from the xylem be estimated from the root model, and fit for the remaining parameters (γ_c and α_c).

During the ~~fitting process~~calibration step we minimise the sum of squares value between the model's output for plant P uptake and leaf mass values against the experimental data values for ~~each~~ the control and maximum applied P scenario (0 and 90/120 kg P ha^{-1} respectively). With the fitted parameters we then run the model for all applied P scenarios.

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The differences between modelling spring barley and winter barley are the time they are grown for (151 and 313 days, respectively), the initial P profile in the soil (20 mg P l^{-1} decay profile and 16 mg P l^{-1} constant profile, respectively) and leaf growth dependence (also depending upon air temperature for winter barley).

Results

We compare two sets of barley field experimental data against the coupled model, the leaf model (where plant P uptake is given by experimental data) and the root model. The aim is to address the differences between the models and how well they fit the experimental field data for barley.

First we compare the values for plant P uptake between the root and coupled model for spring barley at three different growth stages, GS31, GS45 and GS91 for seven applied P rates (0, 5, 10, 20, 30, 60 and 90 kg P ha^{-1}; Figure 2). The coupled model estimates higher plant P uptake compared to the root model, better fitting the experimental data; staying within one standard deviation except at high applied P rates (30, 60 and 90 kg P ha^{-1} at GS31, 20, 60 and 90 kg P ha^{-1} at GS45 and 30 and 60 kg P ha^{-1} at GS91). The feedback effect within the coupled model enables the root structure to become larger than in the root model and therefore the roots explore more of the soil and hence achieve an increased plant P uptake ~~(Figure 8)~~. The final model estimate (GS91) is more accurate than the earliest (GS31) due to not capturing the effects of possible lateral root proliferation due to higher applied P rates (Drew, 1975). Early differences are averaged out as the root system grows.

When considering plant P uptake in winter barley, the coupled model behaves similarly to the root model (Figure 3). At GS92, both models under-predict plant P uptake for the same reasons as stated in Heppell *et al.* (2015); the P profile is depleted which limits the amount of P available for uptake, and perhaps the total amount of P in the soil was different to that estimated by the one soil test for the whole site (Olsen P index 1). The effect of slow release P pools in the soil was not taken into consideration due to the fact experimental data for this phenomenon was not available.

By coupling the root model with the leaf model we are able to compare measured leaf mass values against the coupled and leaf model only for both spring barley (Figure 4) and winter barley (Figure 5) for different applied P rates. The coupled model accurately predicts leaf mass at GS91 for spring barley, however it estimates a more average value for earlier growth stages; not distinguishing any differences between applied P rates. The large errors bars in the experimental leaf mass data are possibly due to field variation, making it hard to distinguish any differences between applied P rates, especially at later growth stages (the experimental differences are not statically significant). In addition, the variation in experimental plant P uptake values for GS31 is less than for GS91 (18% to 24%), implying little correlation between early and late plant P uptake (adjusted r^2=0.4). For winter barley, the coupled model is able to match leaf mass at GS39, but vastly underestimates leaf mass at GS92 due to underestimating plant P uptake as mentioned above. The leaf model fits well across all scenarios for spring and winter barley as it takes the known plant P uptake from the experimental data as an input.

The leaf model component allows us to estimate P (Figure 6) and C mass (Figure 7) in the above ground tissue over the growing period of the crop. The estimated P mass is higher in the leaf model compared to the coupled model for both spring and winter barley. The estimated C mass is higher in the leaf model compared to the coupled model for winter barley, but the other way around for spring barley. In the winter barley case, the increased C and P masses in the leaf model are due to higher plant P uptake values (Figure 3 compared to Figure 2) resulting in a larger end leaf mass. For spring barley, C mass in the coupled model begins lower and ends higher compared to the leaf model because plant P uptake by the root system also begins lower and ends higher (P uptake remains constant in the leaf model). The sudden decrease in C and P mass, for winter barley, around the 250 day mark is due to the enforced halting of the root growth rate.

The root growth rate is affected by C mass (spring barley) and also temperature (winter barley); therefore different final root lengths can be observed between model simulations (Figure 8). The

295 leaf model created a longer root length compared to the coupled model in the winter barley
296 scenario due to the early differences in C mass. For spring barley, the early C mass values for the
297 coupled and leaf model were similar resulting in almost identical root growth rates and hence final
298 root lengths. As C mass increases above a certain value any differences are masked when affecting
299 the root growth rate. There was little difference in root length between the two different fertiliser
300 applications (0 and 90/120 kg P ha^{-1}), the largest being between the coupled model for winter barley
301 GS92. Due to the small increase in plant P uptake between scenarios (0 and 120 kg P ha^{-1}) there was
302 little effect on increasing root length via the slow feedback loop created by the addition of the leaf
303 model. Chemotropism effects from adding large amounts of P fertiliser could perhaps explain any
304 differences between plant P uptake values at early growth stages. In the winter barley scenario, as
305 root growth rate was dependent upon temperature, we see periods of no root growth matching
306 periods of low temperature, as expected.

307 Heppell *et al.* (2015) considered the effects of discrete placing of fertiliser within the root zone
308 against incorporating fertiliser throughout the soil for a range of cultivation options (mix 25, 20 and
309 10 cm, inverted plough, minimum tillage and no cultivation) for winter barley at GS92. We do the
310 same in this paper for the new coupled model (Figure 9). We arrive at the same overall conclusion,
311 placing fertiliser rather than incorporating achieves a higher plant P uptake estimate and under a
312 wet climate (x5 flux of water at soil surface), such as in the UK, this difference decreases (9.9% to 0.3%
313 and 9.8% to 4.5%) over no cultivation for a dry and wet climate respectively. Ploughing was also the
314 best cultivation option moving top soil P to a lower depth, making it more accessible to a
315 comparatively larger root system.

316 **Discussion**

317 In order to obtain a more accurate representation of the growth of barley throughout a crop life
318 cycle we have combined a below ground root-soil model with an above ground leaf model. By
319 combining the two models we are able to let an above ground process (photosynthesis) affect a

below ground process (root growth) and vice versa. C is created via photosynthesis in the leaf model (dependent upon leaf mass and P) and stimulates root growth; increased root growth increases plant P uptake and hence leaf mass. This positive feedback effect could explain why crops with early plant P uptake levels grow more vigorously and can produce higher yields (Brenchley, 1929; Boatwright and Viets, 1966; Green *et al*., 1973; Grant *et al*., 2001). Due to possible unfavourable (e.g. dry) weather conditions, maximising early plant P uptake through greater root proliferation is also a good strategy to help ensure continuing capture of soil resources at later stages of growth.

From the modelling work conducted we can postulate that the whole crop model accurately estimates leaf mass at all growth stages given it has accurate estimates of plant P uptake (an average difference of 4.6% for the whole crop model for leaf mass, compared to 15.8% when using values one standard deviation away from the experimental data). Using the calibrated whole crop model we found the optimal fertiliser and cultivation scenario is to use a plough and place the P fertiliser. The largest increase in plant P uptake when placing fertiliser over incorporating fertiliser was 9.6% (plough, dry climate). The difference between incorporating and placing has been long studied and depends upon a range of criteria such as soil P concentration, soil temperature, crop species and price (Devine *et al.*, 1964; Mahler, 2001). Owusu-Gyimah *et al.* (2013) found that applying fertiliser at a depth of 10 cm and 20 cm away from the plant (placed P) gave the best outcome for maize growing under tropical conditions. By placing fertiliser instead of incorporating it throughout the soil the available P is being put where the root system is going to grow hoping to ensure early plant P uptake and a more successful crop. Hence Wager et al. (1986) found that P fertilizer application rates could be halved by placing fertiliser instead of incorporation because the applied P was more efficiently used. However, optimal fertiliser and cultivation methods depend on the initial soil P condition/distribution (Randall and Hoeft, 1988); this includes at the depth at which existing P is initially available within the soil (Heppell *et al.,* 2015).

For modelling across countries it will be important to measure soil available P levels consistently, by either using a common method or a set of common descriptors. Although, an international 'standard' soil extraction method is not necessarily needed; rather employing a basic soil property (e.g. sorption/buffer capacity) would be better to calibrate fertiliser recommendations. Modelling is the most appropriate way to overcome the problems of site specificity in soil P supply that confound current soil P test methods which do not apply to all soil types, i.e. across countries. Countries generally adopt a particular standard method for soil P tests; many different extractants are used. However, these do not necessarily give correlated results, for example across European laboratories (Neyroud and Lischer, 2002; Jordan-Meille *et al.,* 2012). It is possible that a more robust soil test will be developed in the future, that more accurately reflects immediate P availability to roots across different soil types. For example, using Diffusive Gradient in Thin films (DGT) based on soil P diffusion rates (Van Rotterdam *et al.*, 2009; Tandy *et al.*, 2011) or a method that mimics root P acquisition traits (De Luca *et al.*, 2015). The use of more mechanistic approaches to calculate soil available P levels via a more standardised test, or a combination of tests, enhances their applicability across a wider variety of soil types and may lead to more accurate assessment of fertiliser needs (Van Rotterdam *et al.,* 2014). Also, given that patterns of P concentration with depth in soil profiles vary between sites (Jobbágy and Jackson, 2001), it may also be important to assess surface stratification in no-tilled soils or in subsoils. Over-fertilising soils due to inaccurate estimation of requirement, or mis-interpretation of soil P supply through inappropriate tests leads not only to waste of finite reserves of phosphate-rock but also increased risk of P loss to water causing eutrophication (Hooda *et al.,* 2001). By using knowledge about the distribution of P within the soil and by modelling its implications, it should be possible to save on fertiliser costs by implementing better optimised treatments through targeting P use (Yang *et al.,* 2013; Withers et al., 2014). Furthermore, since crop and fertiliser management have long-term effects on topsoil and subsoil P availability (Bolland and Baker, 1998), it will be important to validate the model over several years if it is to improve on current simpler approaches to decision making. Additional model features would

370 be needed, such as effects between cropping seasons, but would make for a more overall
371 accomplished model. We note that the model would have to be calibrated separately for different
372 crops.

373 Although there was little response to P application observed in the field trial in terms of plant P
374 uptake at late growth stages (GS91 for spring barley and GS92 for winter barley), there was a
375 response at early growth stages (GS31 for spring barley and GS39 for winter barley). This early
376 response could imply that there were limiting environmental factors beyond nutritional inputs. Cold
377 and dry conditions in spring are known to inhibit the transport of P from the soil to the root (Grant
378 et al., 2001). However, if the measured 'low' P soil was an underestimation for the total amount of
379 available P in the soil then this could explain the lack of response at harvest observed in the field. In
380 addition, field variation could in part explain the early response to applied P; however as the root
381 system became larger during the latter growth stages any difference in plant P uptake and resulting
382 yield was evened out. Due to the complex nature of cereal physiology (Sylvester-Bradley *et al.*, 2008),
383 an early plant P uptake response does not necessarily indicate a higher final plant P uptake and yield;
384 because the plant compensates by taking up more P later on as temperatures warm up. The slow
385 feedback effect is a good explanation of the long term behaviour of the crop, and estimation of total
386 plant P uptake.

387 Potentially, new ways to improve efficiency use of P can now be developed by combining recent
388 advances in application technology, sensing technology, geo-spatial information and modelling so as
389 to apply P where it is needed and importantly not apply it where it is not needed. Precision farming
390 equipment is being widely adopted; now, its effective deployment depends on whether the vast
391 amount of data available about a given plot of land can be interpreted to improve the precision and
392 decrease the risks compared to current decision making (Sylvester-Bradley *et al.,* 1999). For example,
393 soil nutrient maps, past yield maps, soil and canopy sensors and climate predictions may provide
394 input data for integrated crop models to output quantitative predictions of fertiliser requirements so

395 that application as sowing can be adjusted in real time. However, the more immediate and
396 preliminary prospect is of using simulation models to compare scenarios of possible treatments, to
397 help guide future soil and fertiliser management strategies, and to accompany continuing field
398 testing.

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405 **References**

406 **Barber S (1984)** Soil nutrient bioavailability: a mechanistic approach. Wiley-Interscience.

407 **Bhadoria P, Kaselowsky J, Claassen N, Jungk A (1991)** Soil Phosphate Diffusion Coefficients: Their
408 Dependence on Phosphorus Concentration and Buffer Power. *Soil Science of America Journal*
409 **55**(1):56-60.

410 **Blackmore S (2014)** Address to the Oxford Farming Conference. 8 January 2014. See
411 http://www.ofc.org.uk/videos/2014/vision-farming-robots-2050 last accessed 07/09/2015.

412 **Boatwright G, Viets F (1966)** Phosphorus absorption during various growth stages of spring wheat
413 and intermediate wheatgrass. *Agronomy Journal* **58:**185–188.

414 **Bolland M, Baker M (1998)** Phosphate applied to soil increases the effectiveness of subsequent
415 applications of phosphate for growing wheat shoots. *Australian Journal of Experimental*
416 *Agriculture* **38(8):**865-869.

Brenchley W (1929) The phosphate requirement of Barley at different periods of growth. *Annals of Botany* **43:**89–112.

Brown L (2012) Outgrowing the Earth: The Food Security Challenge in an Age of Falling Water Tables and Rising Temperatures. Taylor & Francis. ISBN 1-84407-185-5.

Conway G, Barbier E (1990) After the Green Revolution: Sustainable Agriculture for Development. Earthscan, London, UK. ISBN: 978-1-84971-930-8.

Cordell D, Drangert J, White S (2009) The story of phosphorus: Global food security and food for thought. *Global Environmental Change* **19:**292-305.

Defra (2010) Fertiliser Manual (RB209), 8th Edition. The Stationary Office, London.

De Luca T, Glanville H, Harris M, Emmett B, Pingree M, De Sosa L, Morena C, Jones D (2015) A novel rhizosphere trait-based approach to evaluating soil phosphorus availability across cromplex landscapes. *Soil Biology and Biochemistry* **88**:110-119.

Déry P, Anderson B (2007) Peak phosphorus. In: Energy Bulletin, 08/13/2007. Post Carbon Institute. Available: energybulletin.net/node/33164.

Devine JJ, Gilkes R, Holmes MRJ (1964) Field experiments on the phosphate requirements of Spring wheat and barley. *Experimental Husbandy* **11**:88-97.

Drew MC (1975) Comparison of the effects of a localised supply of phosphate, nitrate, ammonium and potassium on the growth of the seminal root system, and the shoot in Barley. *New Phytologist* **75**:479-490.

Dunbabin V, Postma J, Schnepf A, Pagès L, Javaux M, Wu L, Leitner D, Chen Y, Rengel Z, Diggle A (2013) Modelling root-soil interactions using three-dimensional models of root growth, architecture and function. *Plant and soil* **372**:93-124.

439 **Foyer C, Spencer C (1986)** The relationship between phosphate status and photosynthesis in leaves.
440 *Planta **167***(3):369-375.

441 **George T, Brown L, Newton A, Hallett P, Sun B, Thomas W, White P (2011)** Impact of soil tillage on
442 the robustness of genetic component of variation in phosphorus (P) use efficiency in barley
443 (Hordeum vulgare L.) *Plant and Soil* **339:**113-123.

444 **Grant C, Flaten D, Tomasiewicz D, Sheppard S (2001)** The importance of early season phosphorus
445 nutrition. *Canadian Journal of Plant Science* **81:**211–224.

446 **Green D, Ferguson W, Warder F (1973)** Accumulation of toxic levels of phosphorus in the leaves of
447 phosphorus-deficient barley. *Canadian Journal of Plant Science* **53:**241–246.

448 **Greenwood D, Karpinets T, Stone D (2001)** Dynamic Model for the Effects of Soil P and Fertilizer P
449 on Crop Growth, P Uptake and Soil P in Arable Cropping: Model Description. *Annals of Botany*
450 **88:**279-291.

451 **Heppell J, Payvandi S, Zygalakis K, Smethurst J, Fliege J, Roose T (2014)** Validation of a spatial-
452 temporal soil water movement and plant water uptake model. *Geotechnique* **64**(7):526–539.

453 **Heppell J, Payvandi S, Talboys P, Zygalakis K, Fliege J, Langton D, Sylvester-Bradley R, Walker R,**
454 **Jones DL, Roose T (2015)** Modelling the optimal phosphate fertiliser and soil management
455 strategy for crops. *Plant and Soil special edition PSP5*. DOI: 10.1007/s11104-015-2543-0.

456 **Hooda P, Truesdale V, Edwards A, Withers P, Aitken M, Miller A, Rendell A (2001)** Manuring and
457 fertilization effects on phosphorus accumulation in soils and potential environmental implications.
458 *Advances in Environmental Research* **5**(1)**:**13-21.

459 **Jeuffroy M, Vocanson A, Roger-Estrade J, Meynard J (2012)** The use of models at field and farm
460 levels for the ex ante assessment of new pea genotypes. *European Journal of Agronomy* **42:**68-78.

Jobbágy E, Jackson R (2001) The distribution of soil nutrients with depth: Global patterns and the imprints of plants. *Biogeochemistry* **53**(1):51-77.

Jones J, Hoogenboom G, Porter C, Boote K, Batchelor W, Hunt L, Wilkens P, Singh U, Gijsman A, Ritchie J (2003) The DSSAT cropping system model. *European Journal of Agronomy* **18:**235-265.

Jordan-Meille L, RubÆk G, Ehlert P, Genot V, Hofman G, Goulding K, Recknagel J, Provolo G, Barraclough P (2012) An overview of fertilizer – P recommendations in Europe: soil testing, calibration and fertilizer recommendations. *Soil Use and Management* **28**(4):419-435.

Keating B, Carberry P, Hammer G, Probert M, Robertson M, Holzworth D, Huth N, Hargreaves J, Meinke H, Hochman Z, McLean G, Verburg K, Snow V, Dimes J, Silburn M, Wang E, Brown S, Bristow K, Asseng S, Chapman S, McCown R, Freebairn D, Smith C (2003) An overview of APSIM, a model designed for farming systems simulation. *European Journal of Agronomy* **18**(3-4):267-288.

Kuchenbuch RO, Buczko U (2011) Re-visiting potassium- and phosphate-fertilizer responses in field experiments and soil-test interpretations by means of data mining. *Journal of Plant Nutrition and Soil Science* **174:**171-185.

Lohry R (1998) Surface Banding superior To Broadcasting on Reduced-Till. Fluid Journal **22**:14-18.

Lynch J (2007) Roots of the second green revolution. *Australian Journal of Botany* **55:**493-512.

Mahler R (2001) Fertilizer Placement. CIS. Soil Scientist, Department of plant, Soil, and Entomological Sciences, University of Idaho.

Neyroud J, Lischer P (2002) Do different methods used to estimate soil phosphorus availability across Europe give comparable results? *Journal of Plant Nutrition Soil Science* **166**(4):422-431.

Nye P, Tinker P (1977) Solute movement in the soil-root system. Blackwell Science Publishers.

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Owusu-Gyimah V, Nyatuame M, Ampiaw F, Ampadu P (2013) Effect of depth and Placement Distance of Fertilizer NPK 15-15-15 on the Performance and Yield of Maize Plant. *International Journal of Agronomy and Plant Production.* **4**(12):3197-3204.

Randall G, Hoeft R (1988) Placement Methods for Improved Efficiency of P and K Fertilizers: A Review. *Journal of Production Agriculture* **1**(1):70-79.

Roose T, Fowler A, Darrah P (2001) A mathematical model of plant nutrient uptake. *Mathematical Biology* **42**(4):347–360.

Roose T, Flower A (2004a) A model for water uptake by plant roots. *Journal of Theoretical Biology* **288**:155-171.

Roose T, Fowler A (2004b) A mathematical model for water and nutrient uptake by plant root 567 systems. *Journal of Theoretical Biology* **288**:173-184.

Selmants P, Hart S (2010) Phosphorus and soil development: Does the Walker and Syers model apply to semiarid ecosystems? *Ecology* **91**(2):474-484.

Sylvester-Bradley R (1991) Modelling and mechanisms for the development of agriculture. Aspects of Applied Biology 26, The Art and Craft of Modelling in Applied Biology, 55-67.

Sylvester-Bradley R, Lord El, Sparkes D, Scott RK, Wiltshire JJ, Orson JO (1999) An analysis of precision farming in Northern Europe. *Soil Use and Management* **15**:1-9.

Sylvester-Bradley R, Berry P, Blake J, Kindred D, Spink J, Bingham I, McVittie J, Foulkes J (2008) The wheat growth guide, Spring 2008, 2nd edition. HGCA, London 30pp http://www.hgca.com/media/185687/g39-the-wheat-growth-guide.pdf, last accessed 12/09/2014.

Tandy S, Mundus S, Yngvesson J, de Bang T, Lombi E, Schjoerring J, Husted S (2011) The use of DGT for prediction of plant available copper, zinc and phosphorus in agricultural soils. *Plant and Soil* **346**(1-2):167-180.

Thornley JH (1995) Shoot: root allocation with respect to C, N and P: an investigation and comparison of resistance and teleonomic models. *Annals of Botany* ***75***(4):391-405.

Vaccari D (2009) Phosphorus: a looming crisis. *Scientific American* **300:**54-49.

Valkama E, Uusitalo R, Turtola E (2011) Yield response models to phosphorus application: a research synthesis of Finnish field trials to optimize fertilizer P use of cereals. *Nutrient Cycling in Agroecosystems* **91**:1–15.

Van Genuchten M (1980) A closed-form equation for predicting the hydraulic conductivity of unsaturated soil. *Soil Science Society of America Journal*, **44**(5):892-898.

Van Rotterdam A, Temminghoff E, Schenkeveld W, Hiemstra T, Riemsdijk W (2009) Phosphorus removal from soil using Fe oxide-impregnated paper: Processes and applications. *Geoderma* **151**(3-4):282-289.

Van Rotterdam A, Bussink D, Reijneveld J (2014) Improved Phosphorus Fertilisation Based on Better Prediction of Availability in Soil. International Fertiliser Society, Proceeding 755, ISBN 978-0-85310-392-9.

Vance C, Uhde-Stone C, Allan D (2003) Phosphorus acquisition and use: critical adaptations by plants for securing a non-renewable resource. *New Phytologist* **157:**423-447.

Wager BI, Stewart JWB, Henry JL (1986) Comparison of single large broadcast and small annual seed-placed phosphorus treatments on yield and phosphorus and zinc contents of wheat on Chernozemic soils. *Canadian Journal of Soil Science* **66**:237−248.

Wissuwa M, Gamat G, Ismail AM (2005) Is root growth under phosphorus deficiency affected by source or sink limitations? *Journal of experimental botany* ***56***(417):1943-1950.

Withers PJA, Sylvester-Bradley R, Jones DL, Healey JR, Talboys PJ (2014) Feed the crop not the soil: rethinking phosphorus management in the food chain. *Environmental Science and Technology* **48:**6523-6530.

Withers PJA, van Dijk KC, Neset T-SS, Nesme T, Oenema O, Rubæk GH, Schoumans OF, Smit B, Pellerin S (2015) Stewardship to tackle global phosphorus inefficiency: The case of Europe. *AMBIO* 44 (Suppl.):S193-S206.

Yang X, Post W, Thornton P, Jain A (2013) The distribution of soil phosphorus for global biogeochemical modeling. *Biogeosciences Discussions* **9**(11):16347-16380.

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570 **Table 1: A list of the parameters used for the 3 models: leaf, root and coupled.**

Parameter	Definition	Value	Units
Leaf Model (Values from Thornley, J. H., 1995)			
k_G	Leaf growth rate constant	1000	$\left(\frac{\text{kg C}}{\text{kg Leaf}}\frac{\text{kg P}}{\text{kg Leaf}}\text{day}\right)^{-1}$
k_{litt}	Leaf litter rate constant	0.05	day^{-1}
k_{mlitt}	Leaf litter Michealis-Menten constant	0.5	kg Leaf
k_C	Photosynthesis constant	0.1	$\frac{\text{kg C}}{\text{kg Leaf}}\text{day}^{-1}$
k_M	Leaf self-shading constant	1	kg Leaf
J_C	Carbon product inhibition constant	0.1	$\frac{\text{kg C}}{\text{kg Leaf}}$
f_c	Fraction of C used for leaf growth	(fitted)	$\frac{\text{kg C}}{\text{kg Leaf}}$
f_p	Fraction of P used for leaf growth	(fitted)	$\frac{\text{kg P}}{\text{kg Leaf}}$
k_1	P used for photosynthesis	(fitted)	$\frac{\text{kg Leaf}}{\text{kg P}}$
k_p	P:C ratio for photosynthesis production	0.005-0.05	$\frac{\text{kg P}}{\text{kg C}}$
β_p	Rate of P output to phloem	0	$\frac{\text{kg Leaf}}{\text{day}}$
F	Rate of P entry from xylem	Taken from barley experimental data or root model output	$\frac{\text{kgP}}{\text{day}}$
A_T	Air temperature	Taken from Local	$°C$

		Met office MIDAS stations	
β_c	Rate of C output to phloem	(fitted)	$\frac{\text{kgL}}{\text{day}}$
s_1	Air temperature slope constant	(fitted)	-
s_2	Air temperature transition constant	(fitted)	$°C$
Root-Soil Model (values from Heppell *et al.,* 2015)			
D_0	Water diffusivity	10^3	$\text{cm}^2\text{day}^{-1}$
K_s	Water hydraulic conductivity	5	$\text{cm}^2\text{day}^{-1}$
D_f	P diffusivity in free water	10^{-5}	$\text{cm}^2\text{day}^{-1}$
d	Impedance factor	2	-
a	Main order root radius	0.085	cm
a_1	first order root radius	0.060	cm
k_r	Root radial water conductivity	$7.85*10^{-6}$	$\text{m}^2\text{s}^{-1}\text{MPa}^{-1}$
k_z	Root axial hydraulic conductivity	$1.198*10^{-2}$	$\text{m}^4\text{Pa}^{-1}\text{s}^{-1}$
ψ_1	Density of first order roots	2.33	cm^{-1}
p_r	Root internal xylem pressure	1	Pa
p_c	Characteristic suction pressure	0.0232	MPa
L_0	Max length of main order root	150	cm
L_1	Max length of first order root	7.9	cm
L	Root tip position	0-L_0	cm
b	Buffer power	23.28	-
θ	Angle between the main root and first order branches	60	degrees
ϕ	Porosity of soil	0.3	-
p_r^0	Initial root internal xylem pressure	1	Pa

λ_1	Root internal xylem pressure parameter	$2.7*10^{-3}$	Pa/ degC
λ_2	Root internal xylem pressure parameter	$8.46*10^{-4}$	Pa/% humidity
λ_3	Root internal xylem pressure parameter	$7.9*10^{-2}$	Pa
δ	Flux of water parameter	$2.69*10^{-2}$	-
α	Flux of water parameter	$1.2*10^{-6}$	m s^{-1} of water
β	Flux of water parameter	$2.22*10^{-6}$	m s^{-1} of water/degC
γ	Flux of water parameter	$5.35*10^{-4}$	m s^{-1} of water/ m s^{-1} of air
E	Flux of water parameter	$5*10^{-4}$	m s^{-1} of water
l_w	Bottom of the soil	200	cm
Coupled Model			
γ_C	Root carbon growth parameter	(fitted)	-
α_c	Strength of carbon effect on root growth	(fitted)	-
A	Strength of temperature dependence on root growth rate	0.0780	-

571

572 **Table 2: The fitted parameter set for the leaf and coupled models, for spring barley and winter**

573 **barley.**

Parameter		**Value for Spring barley**	**Value for winter barley**
Leaf Model	β_c	0.0001	0.0001

	k_1	100	859
	f_c	0.5	0.5
	f_p	$7*10^{-4}$	$1.6*10^{-3}$
	s_1	n/a	20.78
	s_2	n/a	-1.446
Coupled model	γ_C	$1.30*10^{-5}$	$1.31*10^{-4}$
	α_c	1	1.982

574